PHYLOGENETIC ANALYSES OF THE GENUS *BAPTISTONIA* (ORCHIDACEAE: ONCIDIINAE) SENSU LATO BASED ON MORPHOLOGICAL CHARACTERS

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ABSTRACT

Relationships within *Baptistonia* are estimated based on phenetic and cladistic analyses of 47 morphological characters. The analyses support monophyly of *Baptistonia*, but without strong bootstrap support. Some supraspecific taxa supported by the analyses are discussed.

RÉSUMÉ

On présente, sur la base d'une analyse phénétique et cladistique de 47 caractères morphologiques, les relations de parenté entre les espèces de *Baptistonia*. L'étude soutient le caractère monophylétique du genre, avec cependant de faibles valeurs de bootstrap. Quelques taxons supraspécifiques, suggérés par l'analyse, sont discutés.

Key Words: *Baptistonia*, Brazil, *Gomesa*, Orchidaceae, Oncidiinae, phylogeny

INTRODUCTION

The genus *Baptistonia* was founded in 1877 by Barbosa Rodrigues based on a single species: *B. echinata* Barb. Rodr. Soon after the concept was published, it was generally neglected. Kränzlin (1922), in his revision of the entire subtribe Oncidiinae, placed the species in the genus *Oncidium* Swartz. However, Pabst and Dungs (1977), in their work on the Orchidaceae of Brazil, conserved Barbosa Rodrigues' monospecific genus.

Chiron and Castro Neto (2004) noted that the characteristic vegetative and floral structures of the plants of the section *Waluewa* (Regel) Schltr. of the genus *Oncidium* are close to those of *Baptistonia echinata*, and that all species involved are endemic to the southeastern part of Brazil. Consequently they transfered the species of section *Waluewa* to the genus *Baptistonia*. The thus enlarged genus now comprises twenty one species and two natural hybrids.

DNA sequence data has shown that the species involved are distinct from those belonging to the true genus *Oncidium* (Williams et al. 2001; Chase et al. 2005). This data also seems to indicate that these species form a monophyletic group which is distinct from its neighboring groups (Faria 2004). It should however be noted that the work of Chase et al. and Faria is based on a limited number of species and that the variations observed in the analyzed sequences are extremely small.

At this time, a study based on the trnS-G region of a large number of members of the genus is in progress. Parallel to this study, however, I also wanted to explore the utility of morphology and anatomy in respect to phylogenetic relationships. Faria (2004) published morphological phylogenetic of seven *Baptistonia* species (less than one-third of the group) but included representatives of various other groups of Brazilian oncidiums. The objective of my study is to complement the work of that author and to estimate the interspecific relationships of all naturally occurring *Baptistonia* taxa at the species level, the hybrids being excluded.

MATERIALS AND METHODS

The anatomical and morphological characters that are presented and discussed below have mainly been obtained through the observation of several live plants of each species. Herbarium material was only utilized whenever live material was not available in any sufficient quantity. The observations were supplemented by data deduced from the original descriptions of the taxa.

The genus *Baptistonia* is closely related to the *Gomesa* alliance, a Brazilian Oncidiinae group comprising the genera *Gomesa* R. Br., *Rodrigueziella* Kuntze and *Rodriguesiopsis* Schltr. In this study, I included four

Gomesa species as outgroup: *G. alpina* Porsch, *G. crispa* Klotzsch ex Rchb.f., *G. recurva* R. Br. and *G. sessilis* Barb. Rodr. The trees were rooted with three species of the genus *Oncidium: O. altissimum* Swartz (the type species of the genus, originating from the Antilles), *O. nebulosum* Lindl. (a mesoamerican species belonging to *Oncidium* section *Oblongata* Kraenzlin) and *O. baueri* Lindl. (another species of the section *Oblongata*, native of the Amazonian forests.) Furthermore, I have added two species that I suspect to be close to the species of the genus *Baptistonia:*

—*Carriella colorata* (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda, which was placed in *Oncidium* section *Waluewa* by Senghas (1997) but elevated to a monospecific genus by Castro Neto and Lacerda (2006), and

—*Oncidium trulliferum* Lindl., close to the plants of the genus *Baptistonia* in respect to its vegetative characters as well as in respect to some of its floral structures, but generally placed in *Oncidium* section *Rostrata* Rolfe.

In view of the work of Faria (2004), no specimens were included belonging to any of the other groups of the *Gomesa* clade (a monophyletic group consisting of the *Gomesa* alliance, *Baptistonia* and many of the Brazilian oncidiums).

All specimens that were studied, with the exception of those belonging to the external *Oncidium* group, are epiphytic plants originating from the moist forests of the *Mata Atlantica*. A list of the 217 specimens studied is given in Appendix 1.

The second important issue to discuss relates to the pertinence of the characters that have been selected for the analysis. Chase (1986) stated that several morphological characters, such as the angle between the labellum and the column, the fusion of the lateral sepals, the general shape of the floral segments, the column arms, and the callus of the labellum, cannot be used for an objective phylogeny. Faria (2004), on the other hand, disagrees with Chase's opinion on this matter. Burns-Balogh and Funk (1986) as well as Freudenstein and Rasmussen (1999) discussed a great number of morphological characters in their cladistic analysis of Orchidaceae. In these articles, however, the utility of the characters was evaluated only in respect to generic relationships, not interspecific. Each of the observable characters may either be invariant within the groups studied (and therefore are of no use for phylogenetic analysis), may vary among species, or—as a third possibility—may even vary within a given species, thus being inconsistent and therefore unsuitable for species-level phylogenetics. Thus, this pertinence of the 69 selected vegetative and floral characters, either microscopic or macroscopic, needs to be discussed, in order to (a) eliminate the unsuitable ones, and (b) decide how many different states of each character retained can be used in the present study. In accordance with the recommendations given by Garcia-Cruz and Sosa (2006) for quantitative characters, I employ the Gap-Weighting (GW) coding method as proposed by Thiele (1993), with a limited number of statistical conditions. In this way, the danger of overweighting certain characters is eliminated. Polarity of character coding is based upon pleisiomorphy of *Oncidium*.

According to van den Berg (unpublished), the Oncidiinae evolved, at the beginning of the Miocene, about 23 million years ago, from an ancestor belonging to the tribe Maxillarieae, itself having diversified from a Mesoamerican ancestor. At that time, South and North America were still separated from each other, the Panamean isthmus having been formed during the Pleiocene. It is generally assumed (Por 1995) that there was an inland sea from the east of what is now Colombia to the Pantanal, isolating the entire eastern part of South America, the sea not being connected with the Atlantic Ocean until the Miocene. Therefore, the Brazilian Oncidiinae, especially the *Gomesa* clade, would have diversified much later, on the basis of an ancestor in Central America. The species of *Oncidium* sensu stricto have their center of distribution in Central America, and they are probably much closer to the common ancestor than the species belonging to the genus *Baptistonia*.

Morphological and anatomical characters considered

According to the above discussion, the following twenty characters were considered but excluded: spacing,

diameter and surface structure of the pseudobulbs; length, shape, color of the leaves, consistency of the lamina, distribution of the stomata, shape of the epidermal cells; length and diameter of the peduncle of the inflorescence, length of sterile bracts, flower density; fusion of the lateral sepals of the flowers, outline and apical shape of the lateral sepals, shape and position of the lateral lobes of the lip, curvature of the column, shape of the stigmatic cavity. Some of them correspond to what Chase (1986) calls "unreliable characters."

A. Pseudobulbs (mature but young)

• Height (*character 01*)

Within any given species, the height of the pseudobulbs may vary. Consequently, I used the maximum height observed. The GW Method, applied with the number of states limited to 2, allows setting a limit of 7 cm to differentiate between species with small or large pseudobulbs.

01–maximum height of pseudobulbs: 1 up to 7 cm—2 more than 7 cm

Assumed evolution: 1 → 2

• Shape in vertical section (*character 02*)

The distinctly elongated shape of the pseudobulbs is characteristic for the genus, but certain species of *Baptistonia* do have pseudobulbs that are elongated-ovoid as in *Gomesa*. For the evaluation of this character I have chosen to use the ratio of height over diameter (H/D), the diameter being measured at the thickest part of the pseudobulb. The scoring, according to the GW method, has three states:

02–Vertical section of the pseudobulbs: 1 ovate (H/D<2)—2 elongated ovate—3 cigar shaped (H/D>4)

Assumed evolution: 1 → 2 → 3

• Shape in horizontal section (*character 03*)

Generally, the horizontal section of the pseudobulbs is rounded, but, in *Baptistonia,* it is sometimes somewhat flattened although never strongly flattened (elliptical). This character is evaluated by the ratio (D/d) of the large diameter over the small diameter of the section, calculated according to the GW method accepting two states:

03–horizontal section of the pseudobulbs: 1 strongly flattened (D/d > 1.5)—2 slightly flattened (D/d < 1.5)

Assumed evolution: 1 → 2

• Margin of pseudobulb in horizontal section (*character 04*)

The pseudobulb in an horizontal section is generally ribbed to entire and this character seems to be a pertinent one at the generic level, although not at the specific level.

04–Margins of the horizontal section: 1 angular—2 intermediate—3 rounded

Assumed evolution: 1 → 2 → 3

• Color (*character 05*)

When observed in their natural state, the plants belonging to the genus *Baptistonia* are easily differentiated from the plants of the genera *Oncidium* or *Gomesa* by the color of their pseudobulbs and leaves. The shade of the green of the pseudobulbs and leaves varies distinctly among these genera. Under cultivation at the same spot, this difference remains, showing that the various shades of green are not adaptations to changing environmental conditions.

05–color of the pseudobulbs and leaves: 1 bright green—2 dark green

Assumed evolution: 1 → 2

B. Leaves

Williams (1974) studied the morphology and the anatomy of the leaves of 80 species belonging to a total of 22 genera of the Oncidiinae. Of those 80 species only 4 belonged to the *Gomesa* clade. He concluded that the leaves offer very few interesting morphological characteristics, but that some anatomic features can be very useful. For the evaluation of those characters in the genus *Baptistonia*, see Chiron and Guiard (in preparation).

• Basal sheaths (*character 06*)
At the generic level this character is useful as, in *Oncidium,* the sheaths are long and leafy, hardly shorter than the real leaves. On the other hand, in *Gomesa*, they are leafy but short and, in *Baptistonia,* they are non-leafy.
06–Basal sheaths: 1 long and leafy—2 short and leafy—3 non-leafy
Assumed evolution: 1 → 2 → 3

• Number of leaves (*character 07*)
The majority of the species of *Baptistonia* show a varying number of leaves per pseudobulb. Therefore, for the present study, I considered the maximum number of leaves for any given species.
07–Maximum number of leaves: 1 more than one—2 a single leaf.
Assumed evolution: 1 → 2

• Stomata density (*character 08*)
The density of the stomata on the abaxial surface of the leaves in the genera *Baptistonia*, *Oncidium* and *Gomesa* varies from one species to the others (Chiron & Guiard, in preparation). Although this density also varies within any given species, the intraspecific variation is much lower than the variation among the species. The density of the stomata in most of the species is between 20 and 45 stomata per mm^2; in the other species studied, the density was higher than 55 stomata per mm^2. This character therefore is pertinent at the generic level.
08–stomata density: 1 ≥ 55 per mm^2—2 < 45 per mm^2
Assumed evolution: 1 → 2

• Shape of the stomata (*character 09*)
The shape of the stomata as observed in *Gomesa* and *Baptistonia* is sub-circular to elliptic, whereby the ratio major axis/minor axis can attain 1.4. Notwithstanding the fact that this character can vary considerably within any given species, the differences among the different species allow scoring for three different states.
09–Ellipticity of the stomata: 1 ≤ 1.05—2 > 1.05 and < 1.2–3 ≥ 1.2
Assumed evolution: 1 → 2 → 3

C. Inflorescence

• Total length (*character 10*)
The total length of the inflorescence varies from one species to another. This character must be measured on adult plants during a normal flowering.
10–length of the inflorescence: 1 distinctly longer than the growths—2 as long as or shorter than the growths
Assumed evolution: 1 → 2

• Direction (*character 11*)
The inflorescences are generally erect, later becoming arched under the weight of the flowers. However, in certain species of the genus *Baptistonia,* they are abruptly folded downward directly above the base and long before the buds begin to form.
11–direction of the inflorescence: 1 upward, more or less arched—2 directly folded downward
Assumed evolution: 1 → 2

• Form (*character 12*)
Generally, the inflorescences are branched. They are, however, unbranched in *Gomesa* and in some *Baptistonia* species.
12– inflorescence: 1 branched –2 unbranched
Assumed evolution: 1 → 2

• Formation of the buds (*character 13*)
In general, the buds start to develop after the inflorescence has more or less reached its final length. This is not so in the genus *Gomesa* and in some other species of the *Gomesa* clade. In those cases, the buds start to

develop as soon as the inflorescence starts to develop within the protection of the leafy sheaths.
13–Formation of the buds: 1 when the inflorescence has attained its length—2 as soon as the inflorescence starts to develop
Assumed evolution: 1 → 2

D. Flowers

• Form (*character 14*)
Depending on the species that is under observation, the flowers of *Baptistonia* can be more or less spread or more or less closed and as such globular. I consider this character potentially pertinent.
14–flower: 1 fully spread (more or less in one plane)—2 quasi spherical (petals and dorsal sepal directed forward).
Assumed evolution: 1 → 2

• Outline (*character 15*)
The outline of the flowers can be distinctly circular or vertically ovate. This was determined by using the ratio (H/W) between height and width of the flowers.
15–Flower outline: 1 circular (H/W ≤ 1.1)—2 vertical (H/W > 1.1)
Assumed evolution: 1 → 2

• Color (*character 16*)
Originally, I had based my color evaluation of the flowers on the visual absence of yellow, red, and green pigmentation. However, even when we attribute but two states to each color, meaning "visible" and "non-visible", we obtain a total of 8 possible states. This is too many states for this type of character. Finally, I have decided to retain three states.
16–Flower color: 1 mainly colored bright yellow and/or dark red—2 pale yellow to whitish with reddish-violet spots—3 yellowish or greenish without any red spotting
Assumed evolution: 1 → 2 → 3

• Floral bracts (*character 17*)
Within the genus *Baptistonia*, this characteristic does not vary much, but long flower bracts are typical for the species of the genus *Gomesa*. The GW coding allowing for 3 states gives:
17–Floral bracts: 1 very short (<1/5 pedicel)—2 short—3 long (> 1/2 pedicel)
Assumed evolution: 1 → 2 → 3

D1. Tepals

• Outline of the dorsal sepal (*character 18*)
This character is partially pertinent within the genus *Baptistonia*.
18–Outline of the dorsal sepal: 1 obovate—2 spathulate
Assumed evolution: 1 → 2

• Degree of concaveness of the dorsal sepal (*character 19*)
Several species of *Baptistonia* have a spoon-shaped dorsal sepal. Therefore, this character seems to be pertinent within the genus *Baptistonia* as well as at the generic level.
19–dorsal sepal: 1 plane—2 cucullate
Assumed evolution: 1 → 2

• Outline of the petals (*character 20*)
In order not to overrate this character, I have coded for only two states.
20–Petals: 1 obovate or claviform—2 notched spathulate to panduriform.
Assumed evolution: 1 → 2

• Apex of the petals and of the dorsal sepal (*character 21*)
The form of the apices of the petals and of the dorsal sepal seems to be characteristic within *Baptistonia*.

21– Apex of the petals and of the dorsal sepal: 1 angular—2 rounded or retuse
Assumed evolution: 1 → 2

D2. Labellum

• Fused (*character 22*)

The labellum may be fused to the base of the column or not.
22–labellum: 1 fused—2 articulated
Assumed evolution: 1 → 2

• Claw (*character 23*)

The presence of a long claw is characteristic for the genus *Baptistonia*. This character, evaluated by the factor R—being the ratio of the length of the claw over the length of the labellum—was GW coded for 3 states.
23–Labellum claw: 1 absent or nearly so (R< 1/20)—2 short (1/20<R< 1/5)—3 long (R> 1/5)
Assumed evolution: 1 → 2 → 3

• Shape of the lateral lobes (*character 24*)

24–Lateral lobes of the labellum: 1 somewhat elongated (rounded, triangular or square)—2 wider than long––3 non-existent—4 very elongated (linear, elongated triangular, or linguiform)
Assumed evolution: 1 → 2 → 3 and 1 → 4

• Direction of the lateral lobes within the labellum plane (*character 25*)

25–Direction of the lateral labellum lobes: 1 to 90° away from the lip axis—2 toward the base of the lip—3 toward the apex
Assumed evolution: 1 → 2 and 1 → 3

• Direction of the lateral lobes in respect to the position of the labellum plane (*character 26*)

26–Lateral lobes: 1 more or less within the plane of the labellum or slightly curved forward—2 at least their basal half distinctly directed backward
Assumed evolution: 1 → 2

• Width of the midlobe (*character 27*)

Evaluated in respect to the width of the labellum at the level of the lateral lobes, this character is variable within the genus *Baptistonia*.
27-Width of the labellum at the level of the midlobe: 1 greater—2 similar—3 smaller in comparison to the width measured at the level of the lateral lobes
Assumed evolution: 1 → 2 → 3

• Shape of the midlobe (*character 28*)

or of the labellum if it is entire. Besides being variable within the genus *Baptistonia*, this character seems to have a certain degree of importance in respect to generic differentiation.
28–Shape: 1 wider than long—2 just about circular or square—3 longer than wide
Assumed evolution: 1 → 2 → 3

• Apex of the labellum (*character 29*)

29–Apex: 1 entire—2 split
Assumed evolution: 1 → 2

• Isthmus of the labellum (*character 30*)

I have accorded a great importance to this character as it is a potential differentiating character at the species level in *Baptistonia*. In fact, the character is stable and specific for groups of species. It overlaps slightly with character 24 (state 3 of character 24 is the same as state 5 of character 30).
30–Isthmus of the labellum: 1 elongate rectangular—2 trapezoidal—3 short and wide with rounded sinus—4 short with triangular sinus—5 absent (labellum undivided)
Assumed evolution: 1 → 2 → 3 → 4 → 5

• Margins at the sinus (*character 31*)
A small number of species show a sinus with indented margins and this character appears to be stable and characteristic.
31–Margins at the sinus: 1 entire—2 irregular
Assumed evolution: 1 → 2

• Callus (*characters 32 to 34*)
Within the genus *Baptistonia*, the callus of the labellum is generally made of three parts: a basal part (on the claw), a center part (between the lateral lobes) and an apical part (on the isthmus and on the midlobe). According to Chase (1986), this is a derived condition in the Oncidiinae. In the species that do not have a claw, the callus has no basal part. In *Oncidium*, the callus does not extend onto the median labellum lobe. In *Gomesa*, the callus is made up of two parallel, longitudinal lamellae, followed by two crests in the apical part of the labellum. The diversity of the structures and their remarkable stability within each species have caused me to retain three distinct characters and have made me accord special importance to the median part.

32–Basal part: 1 absent or not differentiated, not ending in two teeth—2 ending in two well differentiated teeth
Assumed evolution: 1 → 2

33–Median part made up of: 1 a compact construction of several well-developed teeth—2 some kind of verrucose and/or sheeted plate—3 a thick, non-verrucose plate, depressed in the center—4 a thin, smooth, inverted V-shaped plate—5 an inverted Y-shaped crest—6 a construction of small elongated wart-like structures, more or less spaced in two rows—7 two large, low crests—8 two thin, high crests
Assumed evolution: 1 → 2 → 3 → 4 → 5 and: 1 → 6 → 7 → 8
Other character state polarities have been evaluated. This one has been retained because it is most congruent with other characters.

34–Apical part of the callus: 1 absent—2 short (< 1/3 of the midlobe)—3 long (> 1/3 of the midlobe)
Assumed evolution: 1 → 2 → 3

D3. Column
• Slenderness (*character 35*)
This character is variable within the genera studied and seems to be pertinent for the genus *Baptistonia*. It is quantified by the ratio H/W between the height of the column and its width measured below the stigmatic cavity and coded according to the GW method for three states.
35–Column: 1 medium ($2.5 \leq H/W < 4.5$)—2 stocky ($H/W < 2.5$)—3 slender ($H/W \geq 4.5$)
Assumed evolution: 1 → 2 and 1 → 3

• Positioning in relation to the labellum (*character 36*)
This character does not seem to be pertinent within the genus *Baptistonia* where it is remarkably stable, but it is useful to differentiate among the genera.
36–column: 1 in the same line as the labellum—2 at an angle of 90° to the labellum—3 tight against the basal part of the labellum
Assumed evolution: 1 → 2 → 3

• Pubescence (*character 37*)
Pubescence of the column is a character of all species within the genus *Baptistonia*, whereby the degree of pubescence varies. Furthermore, this character is useful for the study of the relationships among the genera.
37–column: 1 glabrous—2 slightly pubescent—3 strongly pubescent
Assumed evolution: 1 → 2 → 3

• Tabula infrastigmatica (*character 38*)
The absence of the tabula beneath the stigmatic cavity is common to all species of *Baptistonia* (although with a regression in *B. uhlii*). It marks an evolutionary step in relation to other genera.

38–tabula infrastigmatica: 1 well-developed—2 slightly developed—3 absent
Assumed evolution: 1 → 2 → 3

• Shape of the wings (*character 39*)
39–wings: 1 independently of their shape, wider than long—2 absent or reduced to two minuscule points—3 longer than wide (sometimes becoming wider at the apex)
Assumed evolution: 1 → 2 and 1 → 3

• Spreading of the wings (*character 40*)
40–wings: 1 opened to 90°—2 absent or opened to 180°—3 parallel or as an arch directed to the front
Assumed evolution: 1 → 2 and 1 → 3

• Hairiness of the stigmatic cavity (*character 41*)
The hairiness of the margins of the stigmatic cavity varies between nearly absent and very dense.
41–hairiness: 1 hairs nearly or fully absent—2 hairs rare and/or short—3 hairs long and dense
Assumed evolution: 1 → 2 → 3

• Presence and shape of an appendix to the anther (*characters 42 to 44*)
The apex of the anther can be rounded or elongated, more or less recurved upward and more or less split into two parts. I have retained three characters to describe this appendix where its absence or presence is incorporated into those three characters.
42–appendix: 1 absent to short—2 long
Assumed evolution: 1 → 2

43–appendix: 1 simple—2 bifid—3 double
Assumed evolution: 1 → 2 → 3

44–appendix: 1 straight—2 recurved
Assumed evolution: 1 → 2

• Viscidium (*character 45*)
The form of the viscidium, measured as the ratio D/d of the large and small diameter of the ellipse, seems to be pertinent at the generic level.
45–viscidium: 1 circular or ovate (D/d<3)—2 elliptic (D/d≥3)
Assumed evolution: 1 → 2

• Tegula (*character 46*)
46–tegula of the pollinarium: 1 larger on the side of the viscidium or equally large on both sides—2 spoon-shaped (larger on the side of the pollinia)
Assumed evolution: 1 → 2

• Margins of the clinandrium (*character 47*)
Well-developed, irregular margins are characteristic for *Baptistonia* but little intrageneric variation can be observed.
47–margins of the clinandrium: 1 only slightly developed—2 extending beyond the anther
Assumed evolution: 1 → 2

The evaluation of these 47 characters has made it possible to develop the data matrix shown in Table 1. This matrix was subsequently exploited in two different methods: parsimony and distances.

Maximum parsimony analysis.—For the first method the phylogeny for the group was obtained by using the software package PHYLIP (see Felsenstein 1989, 1993), which is composed of SEQBOOT version 3.57c, MIX version 3.572c and CONSENSE version 3.56c. The coding of the characters corresponding to the evolutionary hypothesis delineated above resulted in a data matrix (not shown here) of 0 and 1. The software parameters were set as follows:

SEQBOOT: number of replications set to 1000—morphological data

MIX: Successive parsimony method according to Wagner and to Camin-Sokal—set of 1000 replications

CONSENSE: *Oncidium altissimum* set as tree root.

Neither the introduction of a threshold within the algorithm nor the random selection of the species had any significant impact on the results.

Distance analysis.—For the second approach, I have used the software ADE-4 (see Thioulouse et al. 1997) to calculate a distance matrix on the basis of the data matrix given in Table 1 by means of the Manhattan method as performed by the DMAUtil-Quantitative Variables utility, after which the minimal length tree was computed by means of the UPGMA method as provided by the NGStat-Minimal Spanning Tree utility.

RESULTS

In respect to the two non-strict consensus phylogenetic trees obtained with the parsimony method (one for the Wagner parsimony and one for the Camin-Sokal parsimony), it can be noted that: (a) as a general rule, the bootstrap values are weak, some branches being supported by values below 50%; (b) there is a distinct separation of the genera *Gomesa* and *Baptistonia* within the *Gomesa* clade; (c) there are, among the species of *Baptistonia*, 6 small groups of species supported by relatively good bootstrap values (>50%), groups that are referred to as complexes; (d) these diagrams suggest a low level of reliability for the other relationships (*bootstrap* <40%).

I have attempted to define these relationships even further in a second step. For this purpose, the number of taxa was reduced by replacing[1] the species by the corresponding complexes. The characters attributed to any given complex were reconstructed on the basis of the characters of the constituent species as well as on the basis of the evolutionary analysis resulting out of these first diagrams. The topology of the initial trees is respected and the relationships among the different parts are consolidated (higher bootstrap values).

Figure 1 represents the semi-strict consensus tree obtained by the combined operations described above. The bootstrap values for the complexes are those obtained in the first step using the Camin-Sokal method, and the bootstrap values of the higher groupings are those obtained in the second step, using the Wagner method. They are labeled above the branches and relate to the node situated to the immediate right. The nodes supported by bootstrap values below 40% are not reproduced. The numbers related to a branch by a dotted line represent the synamorphies of the node ending that branch.

Even though, as is usual when using a large data matrix, the consistency index remains low (0.29), the retention index is relatively high (0.78). This suggests that, in spite of the fact that there is a great deal of homoplasy in respect to the chosen characters, the synapomorphies are rather numerous (cf. Freudenstein & Rasmussen 1999).

Figure 2 represents the distance tree obtained as described above. Its overall topology is close to that of the tree shown in Figure 1: (a) there is a large distance between the *Oncidium* group and the *Gomesa* group; (b) there is a great distance between these two groups and the rest of the species included in the study; (c) among the latter, we find the group "GM1" as well as the complexes *brieniana*, *silvana*, *pubes*, *leinigii*, *pulchella* and *truncata* shown on Figure 1 (for all the specific names of *Baptistonia*, the taxonomic authorities are given in Appendix 1); (d) *Oncidium trulliferum* and *Carriella colorata* are placed at the base of the genus *Baptistonia*. The following discussion is based on the examination of Figure 1, but is overall compatible with Figure 2.

DISCUSSION

The genera *Baptistonia* and *Gomesa* share a number of characters which are not found in the members of the genus *Oncidium*. However, the present study also stresses the numerous synapomorphies shown by the members of each of the two genera.

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[1]As an alternative way of reduction, we have focused on a single sub-group of species as suggested by the structure of the initial phylogenetic trees. The consolidation of the nodes is similar.

Table 1. Evaluated states for the different characters of species studied.

	B. albinoi	B. brieniana	B. cornigera	B. cruciata	B. damacenoi	B. echinata	B. gutfreundiana	B. kautskyi	B. leinigii	B. lietzei	B. nitida	B. pabstii	B. pubes	B. pulchella	B. riograndensis
01	2	2	2	2	2	1	2	1	2	2	2	2	2	1	2
02	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3
03	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
04	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
05	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
06	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
07	1	1	1	1	1	1	1	2	1	1	1	2	1	2	1
08	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
09	1	1	2	2	?	2	2	1	2	2	2	2	3	2	1
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	B. sarcodes	B. silvana	B. truncata	B. uhlii	B. velteniana	B. widgrenii	C. colorata	G. alpina	G. crispa	G. recurva	G. sessilis	O. baueri	O. nebulosum	O. altissimum	O. trulliferum
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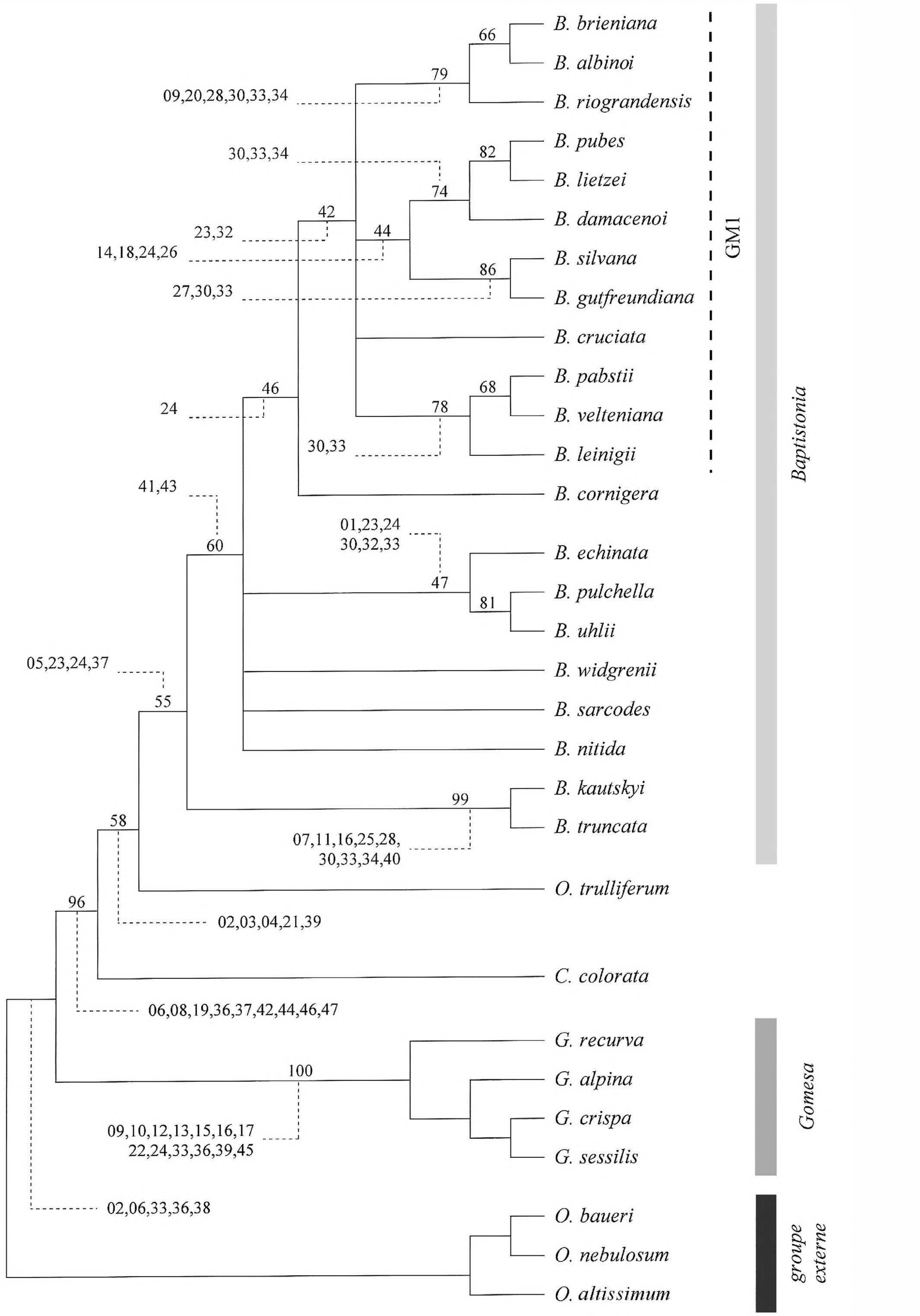

Fig. 1. Semi-strict consensus most parsimonious tree. Figures above the branch lines: bootstrap values. Figures related to the branches by dotted lines: synapomorphies.

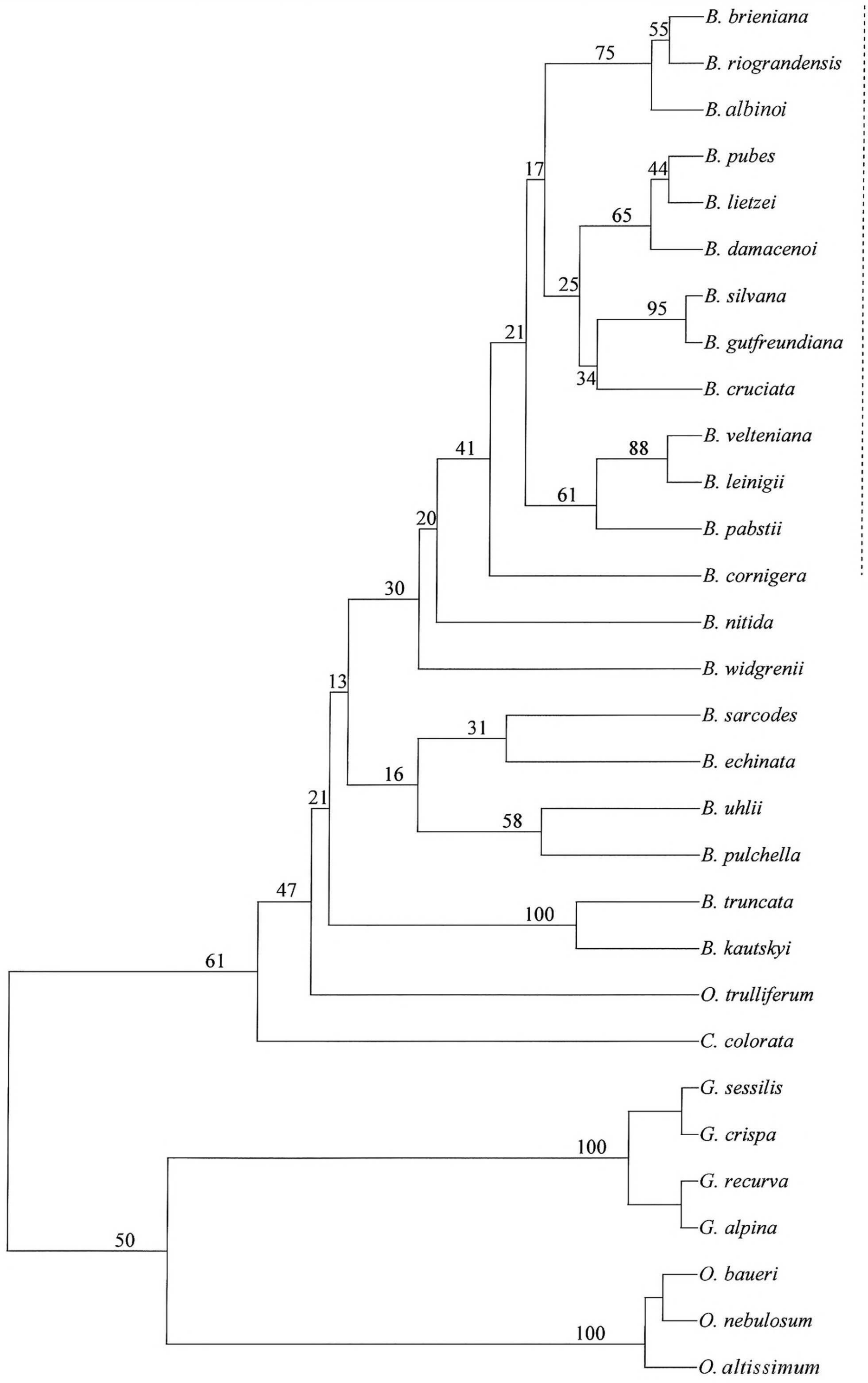

Fig. 2. Distance tree. Figures above the branch lines: bootstrap values.

Synapomorphies of the genus *Gomesa*:
* 09–elliptic stomata;
* 10–short inflorescence;
* 12–inflorescence not branched;
* 13–formation of buds as soon as the inflorescence has been generated;
* 15–vertical shape of the flowers ovate;
* 16–flowers without reddish violet spots;
* 17–floral bracts very long;
* 22–articulated labellum;
* 24–entire labellum;
* 33–callus consisting of two longitudinal crests;
* 36–column pressed against the labellum;
* 39–wings almost non-existent
* 45–viscidium elliptic.

Synapomorphies of the genus *Baptistonia* (with the exception of *Carriella colorata* and *Oncidium trulliferum*):
* 03–pseudobulbs faintly flattened;
* 04–horizontal section of the pseudobulbs rounded;
* 05–pseudobulbs and leaves dark green;
* 06–basal sheaths non-leafy;
* 08–density of stomata low;
* 21–apex of the petals and of the dorsal sepal not angular;
* 37–column pubescent;
* 39–column wings much longer than wide;
* 46–tegula spoon-shaped;
* 47–margin of the clinandrium well-developed.

Other synapomorphies may also be relevant, but with reversals in certain taxa:
* 02–pseudobulbs cigar-shaped (except in *B. uhlii*, *B. truncata*, *B. nitida* and *B. widgrenii*);
* 19–dorsal sepal cucullate (except in *B. uhlii*, *B. widgrenii*, *B. albinoi* and *B. riograndensis*);
* 23–clawed lip (except in the *echinata* complex);
* 42–appendix of the anther long (except in *B. sarcodes*, *B. nitida* and *B. widgrenii*);
* 44–appendix recurved (except in *B. nitida* and *B. sarcodes).*

Finally, we may note the evolutionary steps shown by the two genera in relation to the genus *Oncidium*. However, it is not possible to consider them as synapomorphies of the *Gomesa* clade. To do so it would be necessary to ascertain whether the other groups that are part of this clade would share these synapomorphies, a step that would go beyond the scope of this study:
* 02–elongation of the pseudobulbs;
* 06–shortening of the basal sheaths;
* 33–modification of the median part of the callus;
* 36–diminuation of the angle between the column and the labellum;
* 38–disappearance of the tabula infrastigmatica.

Oncidium trulliferum shares 10 of the 16 synapomorphies of the genus *Baptistonia* and seems to be integrated into this genus. This grouping, which could possibly be designated as *Baptistonia* sensu lato, is supported by a bootstrap of 58%. This value is fairly low and is caused by the fact that *Carriella colorata* is found on some of the most parsimonious trees together with one or another group of species belonging to *Baptistonia* sensu lato. *Carriella colorata* is placed within the phylogenetic reconstruction as the sister species of this group, the whole being supported by a bootstrap value of 96%.

I will now review the six complexes mentioned above:

The "*truncata*" complex [*B. truncata* and *B. kautskyi*]: bootstrap value 99%. This complex is defined by five synapomorphies that are found only in this group:
* 16–ground color of the flower is pale;
* 24+25–the lateral lobes of the labellum are short and directed toward the apex of the labellum;
* 30–the isthmus of the labellum is short with triangular sinuses;
* 40–the wings of the column are spread at 180°;

Other characters are shared with some of the other groups:
* 01–pseudobulbs not very tall (shared with the *echinata* complex, with *B. widgrenii* and with *Carriella colorata*);
* 07–pseudobulbs unifoliate (shared with the *pulchella* complex and with *Carriella colorata*);
* 11–inflorescence growing downward (shared with *B. pulchella* and *B. uhlii*);

* 28–width of labellum midlobe equal to its length (shared with the *brieniana* complex);
* 33–median part of the callus made of a thin, smooth, inverted V-shaped plate (shared with the *brieniana* complex, with the *pubes* complex and with *B. cruciata*);
* 34–callus not extending onto the midlobe (shared with *B. cornigera* and with *B. sarcodes*).

According to my analysis, this complex is at the basis of the genus *Baptistonia*, and is separated from the other members by a branch that is relatively well supported (60%) and defined by two synapomorphies:
* 41– stigmatic cavity with more or less long hairs;
* 43–appendix of the anther bifid or double.

The "*silvana*" complex [*B. silvana* and *B. gutfreundiana*]: 86%. This group is defined by a combination of shared characters each of which can also be found in other species:
* 18–dorsal sepal spathulate (shared with the *pubes* complex and with *B. nitida*);
* 24–lateral lobes of the labellum much longer than wide (shared with the *pubes* and *brieniana* complexes as well as with three other species);
* 26–base of the lateral lobes distinctly folded backward (shared with the *pubes* and *pulchella* complexes, and with *B. cruciata*);
* 27–labellum midlobe wider than the width of the labellum as measured over the lateral lobes (shared with *B. nitida*);
* 30–isthmus of the labellum short and wide with rounded sinuses (shared with *B. sarcodes*, *B. widgrenii* and with the *echinata* complex);
* 33–median part of the callus consisting of a thick, non-verrucose plate that is indented at the center (shared with *B. cornigera*).

The "*pulchella*" complex [*B. pulchella* and *B. uhlii*]: 81%. One synapomorphy:
* 43–appendix of the anther is bifid;

and shared characters, also found in other species:
* 07–pseudobulbs unifoliate (shared with the *truncata* complex and with *Carriella colorata*);
* 10–inflorescence short (shared with *B. truncata* and with *Carriella colorata*);
* 11–inflorescence growing downward (shared with the *truncata* complex);
* 26–base of the lateral lobes of the lip distinctly folded backward (shared with the *silvana* and *pubes* complexes, and with *B. cruciata*);

B. echinata is positioned as a sister species to this complex (bootstrap of 47%) with one synapomorphy:
* 33–median part of the callus made up of two low but wide crests;

and several shared characters, that are, however, also shared with other species:
* 01–pseudobulbs not very tall (shared with the *truncata* complex, with *B. widgrenii* and with *Carriella colorata*);
* 23–claw very short (shared with *B. sarcodes*, *Carriella colorata* and *Oncidium trulliferum*);
* 24–width of the lateral lobes of the lip equal to their length (also found in *B. sarcodes* and *Oncidium trulliferum*);
* 30–isthmus short and wide with rounded sinuses (shared with *B. sarcodes*, *B. widgrenii* and the *silvana* complex);
* 32–basal part of the callus without teeth.

It should be noted, however, that, in respect to the distances, *B. echinata* is the closest neighbor of *B. sarcodes*, and this pair of species is found to be a sister group of the *pulchella* complex.

The "*brieniana*" complex [*B. brieniana*, *B. riograndensis* and *B. albinoi*]: 79%. This group also has no exclusive synapomorphies; it is defined by the following combination of characters:
* 09–circular stomata;
* 20–petals spathulate to panduriform (shared with *B. widgrenii* and the *pubes*complex);
* 28–width of the labellum midlobe equal to its length (shared by the *truncata* complex);

* 30–isthmus of the labellum long and rectangular (shared with the *pubes* complex as well as with *B. nitida* and *B. cornigera*);
* 33–median part of the callus made up of a thin, smooth, inverted V-shaped plate (shared with the *pubes* complex, with the *truncata* complex and with *B. cruciata*);
* 34–apical part of the callus long (shared with the *pubes* complex and with *B. widgrenii*).

The "*leinigii*" complex [*B. leinigii*, *B. pabstii* and *B. velteniana*]: 78%. This group is characterized by two synapomorphies:
* 30–isthmus trapezoidal
* 33–median part of the callus made up of a verrucose, sheeted plate.

The "*pubes*" complex [*B. pubes*, *B. lietzei* and *B. damacenoi*]: 74%. Here again, the group is characterized only by shared characters also found in other species:
* 20–petals spathulate to panduriform (shared with *B. widgrenii*, *Oncidium trulliferum* and with the *brieniana* complex);
* 30–isthmus of the labellum long and rectangular (shared with the *brieniana* complex as well as with *B. nitida* and *B. cornigera*);
* 33–median part of the callus consisting of a thin, smooth, inverted V-shaped plate (shared with the *brieniana* and *truncata* complexes and with *B. cruciata*);
* 34–apical part of the callus long (shared with the *brieniana* complex and with *B. widgrenii*).

In my reconstruction, the *pubes* and *silvana* complexes are sister groups, although with a weak bootstrap value (44%). The two groups are also close to each other in the distance tree. The four synapomorphies that characterize this clade are all characters of low importance:
* 14–flower form;
* 18–dorsal sepal spathulate (shared with the *silvana* complex, as well as with *B. nitida*, *Oncidium trulliferum* and *Carriella colorata*);
* 24–form of the lateral lobes of the labellum;
* 26–base of the lateral lobes distinctly folded backward (shared with the *silvana* and *pulchella* complexes, and with *B. cruciata*).

Together, the *pubes*, *brieniana*, *silvana*, and *leinigii* complexes form a monophyletic group, here referred to as « GM1 ». This group, although weakly supported (bootstrap value: 42%), is characterized by the following synapomorphies:
* 23–nail of the labellum long;
* 32–basal part of the callus ending in a pair of diverging teeth (shared with *B. echinata*).

Baptistonia cruciata is included in « GM1 » but the analyses did not allow a precise clarification of its position. *Baptistonia cornigera* appears as a sister species of this GM1 group (bootstrap of 46%).

Finally, it should be noted that, on the initial consensus tree, *B. widgrenii* appears as a sister species to the entity formed by *B. echinata* and the « *pulchella* » complex, with a very weak bootstrap value (26%) and the shared characters 01 and 30. However, this grouping, besides not supported, would probably be artificial because (a) the structure of the pseudobulbs is very different although the pseudobulbs of *B. widgrenii* are short, and, like those of the other species in this group, much shorter than the pseudobulbs of the other *Baptistonia* species; and (b) the lateral lobes of the labellum are very different although the isthmus is the same. Furthermore, *B. widgrenii* does not share any real synapomorphies with this group. Therefore, the parental relationships of *B. widgrenii* remain to be clarified.

CONCLUSIONS

The present study supports monophyly of *Baptistonia* as defined by Chiron and Castro Neto (2004) as well as its distinctiveness from *Gomesa* based on numerous morphological and anatomical characters.

The proper place of the two species added to the bulk of the specimens to be studied, *Carriella colorata* and *Oncidium trulliferum*, is difficult to define on the basis of this study alone. *Oncidium trulliferum* is positioned at the base of the genus *Baptistonia* and should probably be integrated into that genus (bootstrap of 58%). *Carriella colorata* should rather be regarded as a sister species to the genus. It is, however, better to wait for the results of molecular studies in progress that may clarify this issue.

The phylogenetic relationships within the genus *Baptistonia* are poorly resolved due to the low number of synapomorphies defining the complexes and to homoplasy. However, some monophyletic groups can be distinguished.

Baptistonia kautskyi and *B. truncata* are strongly supported as sister taxa, and are sister to all other species of *Baptistonia*.

The majority of the complexes defined above have been discussed in detail by Chiron and Castro Neto (2005a, 2005b, 2006a, 2006b). One could argue that each of these complexes represents nothing but the expression of the existence of different populations of the same, rather variable species. As many of the combinations of morphological characters that distinguish the members of a complex as well as their distribution zones do not form a continuum but rather disjointed conglomerates, I come, however, to another conclusion.

APPENDIX 1: SPECIMENS EXAMINED

Living material (Vouchers have been deposited in LY (and/or SP when noted) for all plants).

Baptistonia albinoi (Schltr.) Chiron & V.P. Castro: *Chiron 2578, Chiron 0084, Chiron 0085, Chiron 0086*. **B. brieniana** (Rchb.f.) V.P. Castro & Chiron: *Chiron 04604*, *Castro Neto s.n.*, Paraguay *s.n.* **B. cornigera** (Lindl.) Chiron & V.P. Castro: *Chiron 03017*, *Chiron 03035*, *Chiron 02549*, *Chiron 03069*, *Chiron 03008*, *Chiron 03066*, *Chiron 05206*, *Chiron 06576*, *Chiron 07075*, *Chiron 3051*, *Chiron 3052*, *Chiron 3062*. **B. cruciata** (Rchb.f.) V.P. Castro & Chiron: *Chiron 05441*, *Chiron 05446*, *Chiron 05452*, *Zézé s.n.*, *Uhl s.n.*, *Jardin botanique de Lyon 020539*. **B. damacenoi** Chiron & V.P. Castro: *Chiron 03208*, *Chiron 2273*, *Chiron 2589* (type, SP), *Frey746*. **B. echinata** Barb. Rodr.: *AOSP s.n.* ex *Chiron 0042*, *AOSP s.n.* ex *Chiron 0043*, *Jardin botanique de São Paulo s.n.* ex *Chiron 0065* and *Chiron 0066*, *Chiron 2582*, *Chiron 3044*, *Chiron 3045*, *Chiron 3055*, *Chiron 3063*. **B. gutfreundiana** (Chiron & V.P. Castro) Chiron & V.P. Castro: *Chiron 2240*, *Chiron 03414*, *Chiron 05844*, Chiron 05848, *Castro Neto s.n.* ex *Chiron 0058*, *Chiron 3060*, *Castro Neto s.n.* (type, SP). **B. kautskyi** (Pabst) V.P. Castro & Chiron: *Chiron 03194*, *Chiron 04813*, *Chiron 04814*, *Chiron 04816*, *Chiron 05769*, *Chiron 06503*, *Frey 741*, *Frey 1079*, *Caliman s.n.* **B. leinigii** (Pabst) V.P. Castro & Chiron: *Chiron 0101*, *Chiron 07009*, *Chiron 07011*, *Chiron 07012*, *Chiron 07015*, *Chiron 07017*, *Chiron 07018*, *Chiron 07019*. **B. lietzei** (Regel) Chiron & V.P. Castro: *AOSP s.n.* ex *Chiron 0041*, *AOSP s.n.* ex *Chiron 0044*, *AOSP s.n.* ex *Chiron 0045*, *Castro Neto s.n.* ex *Chiron 0046*, *Chiron 06504*, *Chiron 06505*, *Chiron 2273*, *Chiron 2283*, *Chiron 07026*, *Campacci s.n.* **B. nitida** (Barb. Rodr.) V.P. Castro & Chiron: *Chiron 2591*, *Castro Neto s.n.* ex *Chiron 0039*, *Castro Neto s.n.* ex *Chiron 0040*, *Chiron 2592*, *Chiron 2594*, *Chiron 2596*, *Chiron 05532*, *Chiron 06540*. **B. pabstii** (Campacci & C. Espejo) V.P. Castro & Chiron: *Chiron 3042*, *Chiron 3059*. **B. pubes** (Lindl.) Chiron & V.P. Castro: *Chiron 3034*, *Chiron 3036*, *Chiron 3040*, *Chiron 3046*, *Chiron 3047*, *Chiron 3048*, *Chiron 3053*, *Chiron 3054*, *Chiron 06506*, *Chiron 2241*, *Castro Neto s.n.* **B. pulchella** (Regel) Chiron & V.P. Castro: *Chiron 05466*, *Chiron 05487*, *Chiron 05490*, *Chiron 05498*. **B. riograndensis** (Cogn.) V.P. Castro & Chiron: *Chiron 07060, Chiron 07061, Chiron 07062, Chiron 07063, Chiron 07069, Chiron 07070*. **B. sarcodes** (Lindl.) Chiron & V.P. Castro: *Chiron 04850, Chiron 04852, Chiron 05218, Chiron 06570, Chiron 2242, Chiron 2255, Jardin botanique de São Paulo A492*. **B. silvana** (V.P. Castro & Campacci) V.P. Castro & Chiron: *Chiron 2890, Chiron 3049, Chiron 05795, Chiron 05800, Chiron 05807, Chiron 06509, Castro Neto s.n. ex Chiron 0057*. **B. truncata** (Pabst) Chiron & V.P. Castro: *Chiron 05427, Chiron 2785, Chiron 2262, Chiron 2264, Chiron 2769, Chiron 2899A, Chiron 2899B, Chiron 2899C*. **B. uhlii** Chiron & V.P. Castro: *Chiron 2689* (type, SP), *Chiron 06511, Chiron 06512, Chiron 06534*. **B. velteniana** V.P. Castro & Chiron: *Kautskyi s.n.* (type, SP), *Uhl s.n. ex Chiron 0028 and Chiron 0029*. **B. widgrenii** (Lindl.) V.P. Castro & Chiron: *Chiron 0112, Chiron 2243, Chiron 03407, Chiron 03408, Chiron 03409*. **Carriella colorata** (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda: *Caliman s.n., Castro Neto s.n., Chiron 2796, Chiron 06508*. **Gomesa alpina** Porsch: *Jardin botanique de São Paulo s.n.* (SP), *Chiron 05346, Alambari s.n.* **G. crispa** Klotzsch ex Rchb.f.: *Chiron 05462, Chiron 05481, Jardin botanique de São Paulo s.n.* (SP). **G. recurva** R. Br.: *Chiron 03329, Chiron 04683, Chiron 04702, Chiron 04810, Chiron 04811, Jardin botanique de São Paulo s.n.* (SP). **G. sessilis** Barb. Rodr.: *Chiron 04695, Chiron 05388, Chiron 05398, Chiron 05702, Chiron 05715*. **O. altissimum** Swartz: *Chiron 0834, Chiron 1919, Jardin botanique de Lyon s.n.* **Oncidium baueri** Lindl.: *Chiron 02041*. **O. nebulosum** Lindl.: *Chiron 99041*. **O. trulliferum** Lindl.: *Jardin botanique de São Paulo 7028* (SP), *Jardin botanique de São Paulo 11008, Chiron 05249, Chiron 0107, Chiron 0108, Chiron 0109.*

Herbarium material

Baptistonia albinoi: MBM 209548, MBM 99608, MBM 6225, MBM 48898, MBM 48896, MBM 29392, MBM 22869, SP 25185, SP 31577, W-R 35126. **B. brieniana:** W-R 16453 (type de *Oncidium brienianum*), W-R 25704, W-R 7031, P 00430186 (type de *Oncidium verrucosissimum*). **B. echinata:** W-R 10660, W-R 20585, W-R 20586 (type de *Oncidium brunleesianum*). **B. lietzei:** LE

s.n. (type de *Oncidium lietzei*), W-R 25721 (type de *Oncidium hrubyanum*). **B. leinigii:** SP 334938, SP 341393. **B. pubes:** W-R 13085, W-R 28099, W-R 25713. **B. pulchella:** W-R 28923. **B. riograndensis:** ICN-Dutra 925, SP 363181 (type de *Oncidium cassolanum*). **B. sarcodes:** K-Lindley no.84 (type de *Oncidium sarcodes*), MBM 10148, MBM 218812, W-R 44709, WU s.n. **B. widgrenii:** K-Lindley n°50 (type de *Oncidium widgrenii*), SP 46502, W-R 35291, W-R 10423. **Gomesa crispa:** W-R 45401, W-R 45361. **G. recurva**: W-R 34429, W-R 14023, W-R 11818. **Oncidium trulliferum:** MBM 7758, MBM 10717, MBM 48903, MBM 226953, W-R 16262, W-R 6817, W-R 3319.

ACKNOWLEDGMENTS

The author is indebted to Philippe Choler, Université Joseph Fourier—Grenoble I, for his cooperation in the computation of the phylogenetic tree in figure 2; to Guido Braem, University of Maryland, University College Europe, for his helpful discussions; and to Mark Whitten and Norris Williams for providing critical comments on the manuscript. The study of the herbarium materials was made possible by the hospitality demonstrated by the curators of ICN, K, LE, MBM, P, SP, W, and WU to whom I extend my sincere gratitude. My stay at Vienna was supported by the SYNTHESYS Grant AT-TAF-2736. Access to live specimens was made possible through the collaboration of my Brazilian friend Vitorino P. Castro Neto and through some of his local contacts, especially: Carlos Régent, Sergio Gutfreund, Sydney Marçal, and Thomas Adamski. I am deeply indebted to each and every one of them.

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